

## PETIOLAR GLANDS IN THE PLUM<sup>1</sup>

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(WITH PLATES XX, XXI)

True functional glands are present in the plum in three positions: on the leaf serrations, on the leaf base, and on the petiole. In the peach, plum, and cherry, the petiolar glands have been given a place of considerable taxonomic importance. In the course of the fruit breeding work at the Minnesota Agricultural Experiment Station, excellent material became available for a study of the glands in the plum in certain hybrids and pure forms. Since certain questions regarding their variation and morphology appeared to be as yet open, the investigation reported herein was begun.

In a historical review of the taxonomic use of the petiolar glands in the stone fruits, GREGORY (3) showed that the earlier writers had ignored these structures; while later pomologists had made use of them in distinguishing major groups, as in the peach. Other writers, however, questioned the taxonomic value of glands, because of the variation observed in number, shape, and position. From an extensive study of the leading varieties of the peach, GREGORY concluded that on typical shoots the glands were constant, and that in many cases their shape could serve to separate groups of varieties. He arranged the better known peach varieties under three types of glands, reniform, globose, and indistinctive, but pointed out that mixed and transitional types occur.

HEDRICK and others (4) record the gland condition on the petiole and leaf serrations in the descriptions of the principal varieties of plums in New York. Similar data have been brought together for cherries (HEDRICK *et al.* 5) and peaches (HEDRICK *et al.* 6). In the latter work the statement is made that "no one familiar with any considerable number of varieties of peaches

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would attach very great importance to glands in a system of classification."

On the whole, the tendency of later writers has been to attach less significance to glands in classification than has been done by earlier writers. In technical fruit descriptions, or in systematic classifications, it is evident that the value of a character as a distinguishing feature between forms depends largely upon its constancy of expression. Consequently, a statistical analysis was undertaken with the object of determining the number and disposition of glands in certain species and hybrids available.

### Material

Data were first collected in 1914 in the  $F_1$  generation of crosses between Burbank (*Prunus triflora*) and Wolf (*P. americana*), and Abundance (*P. triflora*) and Wolf. The gland condition was subsequently (August 1916) obtained in an additional number of species and interspecific hybrids. Single trees in each case of as nearly uniform age and size as possible were selected, and 400 leaves, on all trees which bore this number, were taken at random from vigorous 1-year shoots. By following this method of collection consistently on trees under fairly uniform growth conditions, the data obtained for the different forms are as nearly comparable as can be obtained under field culture.

There are a number of factors which influence gland development. In general it may be stated that those conditions which produce vigorous vegetative growth favor gland development, since on old trees or on trees subjected to unfavorable growth conditions, the petiolar glands become much reduced, sometimes even disappearing, although normally present in the varieties. On the other hand, position has an influence on glandular development. Leaves borne at the basal position on terminal growth, on fruit spurs or thorns and also in flower buds, typically bear no glands at all or have them less well developed than leaves borne at other points.

The arrangement of the glands (that is, whether opposite or alternate on the petiole or leaf) was not recorded. Glands occur both in pairs and alternately, near together or widely separated,



but since they vary independently on either side of the petiole, their relative position appears to be only incidental.

Variation in gland position and number

In horticultural literature, glands have been described with respect to color, type or shape, size, number, and position. In

TABLE I

SELECTED INSTANCES ILLUSTRATING METHOD OF RECORDING DATA AND SHOWING VARIABILITY OF GLANDS (A) ON DIFFERENT LEAVES WITHIN A VARIETY, (B) WITH REFERENCE TO POSITION ON PETIOLE OR LEAF BASE, (C) WITH REFERENCE TO DIFFERENT VARIETIES, AND (D) WITHIN SAME VARIETY DURING DIFFERENT SEASONS.

NO. BORNE ON		ABUNDANCE X WOLF NO. 35		BURBANK		BURBANK X WOLF NO. 9	
Peti- ole	Leaf	1914	1917	1914	1917	1914	1917
0	0.....	15	38	10	45	44	52
0	1.....	27	35	16	63	25	44
0	2.....	28	37	32	45	28	45
0	3.....		1				
1	0.....	34	40	6	8	25	33
1	1.....	29	33	8	29	63	48
1	2.....	1	16	9	25	9	6
1	3.....				1		
2	0.....	219	188	67	65	141	161
2	1.....	39	10	45	47	49	5
2	2.....	4		33	18	1	1
2	3.....				1		
3	0.....	11	2	55	20	8	4
3	1.....	3		33	17	6	
3	2.....			12			
4	0.....			33	7		
4	1.....	1		24	3	1	1
4	2.....			9	1		
5	0.....			2	2		
5	1.....			3	1		
5	2.....			1	1		
5	3.....				1		
6	0.....			2			
Glands on petiole.....		604	491	919	505	525	437
Glands on leaf.		143	187	321	349	220	202

the plum the globose form is the prevailing type, and the true reniform type is found so seldom that little attention has been given to shape. The color of the mature glands in the plum is dark brown; and since these studies of number and position were made on mature leaves, color characters were also not recorded.



Data taken as to position and number were arranged in the form illustrated in table I, in which each leaf is classified with respect to the position and number of its glands. For instance, in Burbank 67 leaves bore two glands on the petiole and none on the leaf in 1914, and in 1917, 65 leaves fell in this class. A number of other varieties could have been included, but these were selected as typical of the great variability encountered.

Table I shows that in number and position glands are extremely variable on different leaves within a variety, but that the range of variability is fairly typical for each variety. The number of glands borne on the petiole is greater than the number borne on the leaf base, and while the number borne in each position is considerably different from season to season, yet the grouping opposite each class is quite similar in each variety in spite of the fact that the 1917 data were taken from different trees, but of the same clones, from those of 1914. Taking Burbank again as an illustration of variability, it will be seen that some leaves have no glands on either the petiole or leaf, while others bear as many as five on the petiole and three on the leaf. If observations as to gland condition made on a few leaves or herbarium specimens are considered from the standpoint of the variation shown, it will be evident that some caution must be exercised in classifying the gland condition.

Referring to the variability of glands within the species, it will be seen that a similar condition is found to that shown within varieties. A summary of the position and number of glands in all the species investigated is presented in table II, in which the gland condition is given for a total of 3477 leaves.

Four points are of interest in table II: (1) without exception there are more glands borne on the petiole than on the leaf base; (2) when there is one gland present it may be borne either on the leaf base or on the petiole; (3) when two glands are present, the larger number is without exception borne on the petiole; and (4) when more than two glands are present, without exception a strikingly larger number occur on the petiole.

For the convenience of the reader the data presented in table II, with the addition of data from certain interspecific hybrids,



TABLE II  
SUMMARY OF DATA AS TO DISPOSITION OF GLANDS IN ALL FORMS UNDER INVESTIGATION SHOWING RESPECTIVE GLAND NUMBER BORNE ON  
LEAF BASE AND THE PETIOLE IN EACH SPECIES

GLAND NUMBER	P. AMERICANA (WILD); 877 LEAVES STUDIED		P. AMERICANA MOLLIS (WOLF); 400 LEAVES STUDIED		P. BESSEYI; 400 LEAVES STUDIED		P. CERASUS; 400 LEAVES STUDIED		P. DOMESTICA (SHIPPERS' PRIDE); 400 LEAVES STUDIED		P. PENNSYL- VANICA; 400 LEAVES STUDIED		P. SIMONI; 200 LEAVES STUDIED		P. TRIFLORA (BURBANK); 400 LEAVES STUDIED	
	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on petiole	Glands on petiole	Glands on leaf	Glands on petiole	Glands on leaf	Glands on leaf
0.....	624	703	57	364	126	330	48	242	376	210	75	393	17	183	52	167
1.....	128	136	81	33	78	33	55	75	13	95	120	6	25	5	32	134
2.....	122	38	260	3	196	37	245	82	11	93	185	1	107	9	148	98
3.....	3	.....	2	.....	.....	.....	48	1	.....	2	16	.....	17	2	98	1
4.....	.....	.....	.....	.....	.....	.....	2	.....	.....	.....	4	.....	26	1	60	.....
5.....	.....	.....	.....	.....	.....	.....	2	.....	.....	.....	.....	.....	5	.....	9	.....
6.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2	.....	1	.....
7.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	.....	.....



are rearranged in table III, to emphasize the modal class for gland number on the petiole and on the leaf base. It will be seen in all the combinations summarized therein that the mode for gland number on the petiole (with only three exceptions) is two, and that on the leaf base it is zero. In other words, the 2-0 condition shown in figs. I and II is typical in the plum. Thus it appears that the glands in the plum are too variable, both in position and number, for accurate statements concerning their disposition on

TABLE III  
SUMMARY OF GLAND CONDITION IN ALL FORMS STUDIED, SHOWING MODAL CLASS OF GLANDS BORNE ON PETIOLE AND LEAF BASE.

SPECIES OR CROSS	NUMBER OF TREES INCLUDED IN SUMMARY	TOTAL LEAF NUMBER	GLANDS BORNE ON PETIOLE			GLANDS BORNE ON LEAF		
			Number	Mode	Mean	Number	Mode	Mean
Abundance ( <i>P. triflora</i> )	I	400	409	2	I.023	189	0	0.473
Burbank ( <i>P. triflora</i> )	I	400	913	2	2.285	333	0	0.833
Wolf ( <i>P. americana mollis</i> )	I	400	607	2	I.518	39	0	0.010
Abundance×Wolf crosses	38	15200	21956	2	I.440	9125	0	0.600
Burbank×Wolf crosses	22	8000	10406	2	I.300	5028	0	0.628
<i>P. americana</i>	3	877	356	0	0.406	212	0	0.242
<i>P. Besseyi</i> (Sand cherry)	I	400	407	2	I.018	107	0	0.268
<i>P. Besseyi</i> crosses	6	800	3359	2	I.866	788	0	0.438
<i>P. Besseyi</i> × <i>P. hortulana mineri</i> (Compass)	I	400	428	2	I.070	212	0	0.530
Compass crosses	8	1437	2019	2	I.405	514	0	0.357
<i>P. cerasus</i>	I	400	707	2	I.768	242	0	0.605
<i>P. domestica</i> (Shippers' pride)	I	400	35	0	0.088	287	0	0.718
<i>P. domestica</i> × <i>P. americana</i>	I	200	89	0	0.455	112	0	0.560
<i>P. pennsylvanica</i>	I	400	554	2	I.385	8	0	0.020
<i>P. Simoni</i>	I	200	438	2	2.019	33	0	0.165

any other basis than that of a statistical analysis. Other characteristics of glands, however, may be of distinctive value, and gland disposition may be sufficiently different and characteristic for a variety or species to be of taxonomic value. The outstanding feature of the data on the disposition of glands is that the mode for gland number on the petiole, with three exceptions, falls on two, and that the mode for the number borne on the leaf base in every instance is zero. This condition obtains notwithstanding the great diversity in the forms under investigation, and even in the three exceptions to a modal class of two on the petiole, the mode



was zero. This is significant in view of the fact that these three forms, *P. americana*, *P. domestica* (Shippers' pride), and *P. domestica* × *P. americana*, showed the greatest suppression of the glands of any of the forms included in this investigation. This condition will be given even greater emphasis in view of the connection found to exist between glands and the vascular system of the leaf.

### Connection of petiolar glands with vascular system

With the status of the glands as to number and position shown by the statistical analysis in mind, it now remains to be seen whether or not there is a basic cause for the predominance of the 2-0 frequency.

The leaf trace in the plum has three bundles of conducting tissue at its departure from the vascular cylinder of the stem, which cause three gaps in the woody cylinder. The central bundle extends up the petiole, through the blade, and branches successively at the large lateral veins. The outer bundles give rise to strands which run along the upper side of the petiole, forming pronounced ridges on either side. These strands run directly to the petiolar glands, or to the large ones borne on the leaf base, and terminate there. The term petiolar gland, therefore, will be used in this connection to include both. The lateral strands are shown in fig. 30, which was drawn from a young leaf, and they are equally conspicuous whether the glands are borne on the leaf base or some distance down on the petiole. Where there is more than one gland on either side of the petiole, branches from the lateral strands connect with them.

On the other hand, the glands of the leaf serrations have a distinctly different vascular connection. Instead of being connected by branches with the lateral strands, glands in this position have their vascular connections with the central bundle through the lateral veins. It appears, therefore, that on the basis of differences in their vascular connections the petiolar glands and the glands borne on the serrations can be placed in two distinct classes. Other considerations also support this view. The petiolar glands are much larger than those on the serrations and may show differences in shape, such as the reniform or necked types,



which would readily differentiate them. Also under orchard conditions the glands on the petiole may be active much later in the season. That there is no relation between the glands in the two positions is further shown by the fact that in some species, as in *P. americana*, glands are typically absent on the serrations but present on the petiole or leaf base.

Glands which could not readily be classified as belonging to either the leaf serrations or the petiole were not numerous, consequently error from this cause has not entered to any appreciable extent into the statistical classification. There was also little difficulty in determining whether glands were borne on the petiole or leaf base, since in most cases there was no leaf tissue between the glands and the base of the blade. When leaf tissue was so present they were classed as being borne on the leaf base.

The question now arises as to whether the structure of glands on the petiole is similar to that on the leaf base. GREGORY (3) showed that glands borne on the petiole and leaf base in the peach were true glands, the upper part being composed of long rectangular cells rich in cytoplasm, and with large nuclei, while the central part is made up of parenchyma cells characteristic of glandular tissue, into which extend ramifications of conductive tissue. The structure of the glands in the plum borne on both the petiole and serrations has been examined on leaves just emerging from the bud, and on mature leaves with vigorous active glands, and is found to be similar to that reported by GREGORY in the peach.

The similarity in structure between the glands borne on the petiole and on the serrations led GREGORY to suggest that the former arose from the latter. Such an origin would imply that both are of the same rank, and that the tissue of the leaf blade is more or less indeterminate with that of the petiole, and would be in accord with the condition of the petiolar glands in some species of willow, notably *Salix lucida* (fig. 10), in which the glands are minute, numerous, and crowded together at the leaf base, suggesting a proliferation of leaf tissue along the petiole.

From these considerations it appears that there is justification for regarding the glands of the petiole, and the larger ones borne



on the leaf base, as of the same structure but of different rank from those borne on the serrations. This is in keeping with the evidence presented in the statistical analysis in which the number two figured so prominently, that is, two glands on the petiole and none on the leaf base, or one in either position, or less frequently, two on the leaf base. The points emphasized are of significance from the standpoint of phylogeny, and will be given greater emphasis from that standpoint.

**Phylogeny of leaf as indicated by glands, vascular system, stipules, and abscission layers**

There are structures other than the glands which are significant from the standpoint of the ancestral type of leaf in *Prunus* and related genera. COOK (1) called attention to a joint in the leaves of Amygdalaceae "just above the insertion of the stipules," and states that the "basal section of the leaf below the joint" has a separate abscission from that of the leaf proper. This "basal section" is regarded as belonging to the leaf on the basis of the attachment of the stipules to it, although the stipules themselves absciss early, and hence "the persistence of the base of the leaf" has been overlooked. GOEBEL (2) characterizes stipules as "appendages arising at the insertion of a leaf, attached either wholly to the petiole or to the stem, or to both." SINNOTT and BAILEY (12) regard the stipules as arising through the stimulus of the growth of the lateral leaf trace, and although they are morphologically integral parts of the leaf, in some exstipulate families having trilacunar nodes, they are represented by mere swellings opposite the leaf trace. In some stipulate genera with opposite leaves, as *Viburnum*, the stipules arise midway between the insertion of the petioles, apparently directly from the stem. COOK also states that in Texas this basal section in the peach may remain alive for a year or two and then wither away; while in Maryland it lives through the winter and separates in the spring, leaving a fresh green scar.

In most of the plums studied in this investigation, this structure does not separate at all, but may be clearly observed (the petiole scar with its three bundle scars, and the two stipule scars at its



sides) on 3-year or even 4-year-old wood. Some vestige of it often remains a year or two longer, but usually after this time it begins to slough off.

It was not until some young trees of *Amygdalus Davidiana*, which were making an extremely rapid spring growth, were examined that the separation which Cook described was found. Ordinarily it requires some effort to remove the dry scalelike remnant left after the fall of the leaf, and usually there is more or less tearing of the bark; but in the case of *Amygdalus Davidiana* this structure separated easily and clearly when started with a knife point. In many cases after the rapid spring growth it cracked and separated without any outside stimulus, and later a large proportion fell as a result of further enlargement at the node. The condition is represented in fig. 5, which shows the separating scale, and fig. 31, which shows its structure in greater detail.

Examination of rapidly growing shoots of other *Prunus* species showed that a similar separation may take place, especially in some of the *P. Besseyi* × *P. triflora* hybrids, although in no case quite so sharply as in *Amygdalus*. At least a partial explanation of the fact that the separation of the scar scale occurs in some species of *Prunus* and not in others, can be made on the basis of the character of the swelling of the node below the leaf insertion. When it is straight in outline, it makes an acute angle with the line of the shoot and terminates in the leaf scar along a narrow ridge, as in *Amygdalus* (fig. 5). The rapid growth in spring of tissue underneath forces off the dead scale at the apex. If, however, the node is swollen, with a rounded profile, and the leaf scar is well buttressed below, as in the extreme type shown in fig. 4, the scale does not separate, and cannot be removed without tearing the bark. In either case, whether separation is immediate or delayed, it is only the shedding of dead tissue, just as bark is shed, and is done without the aid of a definite abscission zone (LOYD 9), and consequently is not true abscission.

A search for corroborative evidence as to the nature of this structure showed that in a number of genera it is not uncommon for clean cut separation of a scar scale to occur when rapid growth



begins. Some of the species which show the separation of the old leaf scar more clearly even than *Amygdalus* are *Shepherdia argentea*, *Cornus stolonifera*, *Tilia americana*, *Rhamnus cathartica*, and *Celtis occidentalis*, the first two of which are illustrated in figs. 16 and 17. All of these have simple leaves and lack petiolar glands, and *Cornus* and *Shepherdia* are exstipulate and have entire leaves, which, according to SINNOTT and BAILEY (11, 12), is an advanced state of node and leaf morphology. Hence we must regard the structure to which the stipules and petiole in *Prunus* are articulated, not as an additional foliar element, but as an outgrowth from the stem; and therefore abscission of this kind does not necessarily indicate an additional foliar element.

The manner of insertion and abscission of the stipules in the plum furnishes additional evidence that the structure described by COOK as a persistent leaf base is in reality a part of the stem, and that the leaves of Amygdalaceae cannot therefore be jointed.

In some Rosaceous genera, as *Potentilla* and *Rosa*, the stipules are adnate to the petiole, forming a somewhat sheathing base, and fall with the leaf. In others, as *Pyrus* and *Prunus*, the stipules are separate, or nearly separate, from the petiole, and absciss soon after the buds unfold. In *Prunus* the stipules usually drop long before the leaf, but occasionally they persist throughout the growing season, and even over winter, in vigorous, late growing branches in which cold weather has stopped further growth. The point of normal abscission is illustrated in fig. 32 (*P. hortulana mineri*). The stipules, like the petiole, separate at a definite abscission layer at their base (figs. 1, 2). As COOK pointed out, the joint of the latter lies above the stipules, that is, distally to them, although since the abscission lines of the petiole and the stipules form a sort of crescent with the points upward, a face view of the stem shows the stipule scars above that of the petiole (figs. 31, 32).

The typical leaves of many stipulate genera of the Rosaceae have stipules adnate to the petiole, forming a more or less sheathing base. This condition is also to be found in the bud scales and the scales transitional to leaves in *Prunus*. Morphologists regard bud scales as relatively primitive in structure, since they have not specialized to serve such varied functions as the leaves themselves.



Accordingly, the bud scales of *Prunus* may be taken as an index of the ancestral leaf type. A series of bud scales and scale leaves grading into true leaves is shown in figs. 18-29, which were taken from a young shoot of the Compass cherry (*P. Besseyi* × *P. hortulana mineri*).

It may clearly be seen that in the outer scales the stipules are represented by blunt lobes, as large as the central lobe which represents the leaf blade. The inner scales show progressive reduction in size of the lateral lobes and increase of the middle one, accompanied by differentiation into stipules and lamina. It will be noted, also, that there is progressive splitting of the stipules from the petiole. In the mature leaf of the plum this splitting has progressed to the base of the petiole, so that leaf and stipules have separate abscission, but from one originally continuous abscission layer. *Prunus avium*, as represented by the Dyehouse cherry, is at a somewhat intermediate stage. In the leaves near the base of a shoot, the stipules are clearly adherent to the petiole, while in the upper leaves they are separate, as in the plum. In all these transitional bud scales separation from the axis is clearly below the stipules, and there is no evidence of an abscission layer above them cutting off the middle lobe or leaf blade (fig. 2); hence the stipules in the plum must be regarded morphologically as integral with the leaf base, although the course of development separates them from the petiole in the mature leaf.

It remains to interpret the structure of the petiolar glands in relation to a more primitive type of leaf. Their organization and their occasional proliferation into leaflike outgrowths indicate that they are reduced structures. This change from a glandular to a foliar structure was noted by COOK (1), who described the occurrence of "small oblong or spatulate leafy organs on the upper part of the petiole, taking the place of the nectaries" in certain varieties of apricots. A similar transformation has been observed in *Crataegus*, as well as a number of species of *Prunus*, and in some of the apricot hybrids at the Minnesota Experiment Station it is of almost regular occurrence on vigorous shoots of young trees. Some of the variations in this transformation are illustrated in figs. 11-15. The view that the leaves of the Amygdalaceae are



jointed, led COOK to conclude that the ancestral leaf type of this group was compound, the nectaries representing "rudiments of divisions of compound leaves." It should be pointed out, however, that if the modern plum leaf represents the terminal leaflet of an originally compound leaf, the glands, representing reduced lateral leaflets, should be found below the joint by which the terminal leaflet is articulated to the rachis. It is obvious that being situated on the petiole above the joint, they cannot represent lateral leaflets of an ancestral pinnate form. Microscopic sections of the petiole at the leaf base do not show an abscission layer subtending the blade, and the presence of one is not indicated by the normal manner of shedding the leaves. It may be safely concluded, therefore, that the leaf blade of the plum is not articulated to the petiole, as in *Citrus*, *Berberis*, or *Trifolium*. Sometimes, however, if there has been late growth in the fall and the leaves are immature when the first frosts occur, the leaf axis may be broken anywhere from the middle of the blade to the base of the petiole, although most frequently at the juncture of the blade and petiole. In this case the twig enters the winter with a part or all of the petiole adhering at each node, which, however, usually breaks off at the point of normal abscission by spring.

Glands, however, may represent divisions of an alternate divided or pinnatifid leaf, such as *Fragaria*, *Potentilla*, and other genera of the Rosaceae possess. The frequency of the occurrence of two glands suggests a ternate leaf such as that of *Fragaria*. The presence of additional glands may be accounted for on the basis of branching of the lateral bundles, or by the common transition from ternate to quinquefoliate or pinnate leaves (LEWIS 7, 8). Some pinnate-leaved forms of *Potentilla* show reduction of the lower divisions to smaller structures than are the leafy outgrowths in the position of glands in the apricot. Furthermore, the lower divisions are frequently alternate instead of paired, as is also the case with the petiolar glands in *Prunus*.

It will be recalled that in the plum the two lateral bundles which connect with the glands terminate there, and do not contribute extensively to the vascular system of the blade. In ternate leaves which have three strands, the outer two provide the



vascular system of the lateral leaflets, and this is also frequently the case when there are numerous lateral leaflets, as in pinnate forms of *Potentilla*.

On foliar evidence the connection of the stone fruits, whether regarded as a tribe of the Rosaceae or as a separate family, with the Potentilleae is quite direct. The nodal anatomy is the same (SINNOTT and BAILEY 12) and the steps in leaf evolution appear to be: (1) reduction of the lateral leaflets of a ternate or pinnate-divided leaf to petiolar glands; and (2) splitting of persistent adnate stipules from the petiole. In this series *Prunus avium*, with an extensive development of glands, both in number and size, or the apricot with a frequent reversion to leafy structures in place of glands, would stand below *Prunus americana* with its almost glandless petioles. GREGORY (3) regarded the globose gland as more primitive than the reniform, since when normally glandless leaves produced glands, they were always of a globose type. If, however, the trend is toward reduction of glands, the glandless petiole would be the highest type, and the globose condition transitional between it and the reniform.

It has been customary to trace the connection of the drupes with the more primitive Rosaceae through *Spiraea* (RYDBERG 10). Considered on the basis of floral evidence alone, this seems a logical sequence, *Spiraea* being intermediate in form of receptacle and number of carpels between *Potentilla* and *Prunus*. SINNOTT and BAILEY (12) have shown, however, that *Spiraea* is exstipulate and possesses a unilacunar node, while all species of *Prunus* have stipules and a trilacunar node. It would appear that forms with stipules could not be derived from forms which lack them. The relationship of the stone fruits to the true Rosaceae is probably more direct, and on the basis of anatomy there is less reason for separating them as a distinct family than for considering them a well defined and specialized tribe.

### Summary

Examination of over 30,000 leaves belonging to 15 species and interspecific hybrids of the plum shows that two glands typically occur on the petiole, or less frequently on the leaf base.



On the basis of vascular connections the glands on the petiole or leaf base are of a different order of structure from those on the leaf serrations.

The stipules in the plum are morphologically integral with the leaf base, and separate from the stem by a common abscission layer. A portion of the node bearing the leaf and stipule scars is subsequently shed in some species of *Prunus* as in other woody genera; but the portion thus shed is not an additional foliar element.

On the basis of nodal anatomy and the presence of reduced structures, the ancestral type of leaf in the plum is considered to be a ternate lobed or divided simple leaf, the petiole glands representing the suppressed lateral members. In floral structure and nodal anatomy *Prunus* and related genera form a logical series with the Potentilleae, and should be considered as a specialized tribe of the Rosaceae.

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## EXPLANATION OF PLATES XX, XXI

### PLATE XX

FIG. 1.—Section through node showing abscission zone by means of which the leaf is shed; *a*, only abscission zone present.

FIG. 2.—Showing continuous abscission zone (*a*) for stipule and petiole at early stage of growth.

FIG. 3.—Dark line at base of stipule showing point of abscission; note that it is distal to attachment of petiole.

FIG. 4.—Instance of extreme swelling in node below point of abscission of leaf; in such instances scar scale is not shed.

FIG. 5.—Enlarged view of shedding of scar-scale (*a*) in *Amygdalus Davidiana* as result of early spring growth; shedding of this type occurs only when contour of node is relatively flat.

FIGS. 6-9.—Variation in gland position and number; types illustrated are 2-0 (2 on petiole and 0 on leaf base), 1-0, 1-1, and 0-1.

### PLATE XXI

FIG. 10.—Leaf of *Salix lucida* showing glands similar to those of leaf serrations crowded at base.

FIGS. 11-15.—Types of proliferation of petiolar glands into leafy outgrowths.

FIG. 16.—Node of *Shepherdia argentea* showing shedding of scar scale similar to *Amygdalus*.

FIG. 17.—A node of *Cornus stolonifera* showing same as 16.

FIGS. 18-28.—Bud scales and basal leaves from young shoot of Dye-house cherry, presenting series in separation of stipules from leaf blade.

FIG. 29.—Enlarged basal leaf illustrating venation of stipules and leaf blade; note that veins of stipules arise as branches of lateral strands.

FIG. 30.—Petiole showing prominence of lateral bundles in young leaf.

FIG. 31.—Shedding of dead scar scale in *Amygdalus Davidiana* from which stipules and petiole abscissed previous season.

FIG. 32.—Node of young plum stem showing relation of line of abscission in stipule and petiole.